Craig Syms · Geoffrey P. Jones

Soft corals exert no direct effects on coral reef fish assemblages

Abstract Correlations between abundance of organisms and their habitat have often been used as a measure of the importance of particular habitat features. However, experimental manipulation of the habitat provides a more unequivocal estimate of its importance. In this study we quantified how fish communities on small patch reefs covaried with changes in benthic cover habitat features. A random sample of small patch reefs was selected and both fish abundance and habitat measures recorded. Naturally occurring patch reefs could be classed into three habitat types based on their benthic cover. Reefs dominated by massive soft corals were the most abundant (50%), followed by those dominated by rock and soft corals in equal proportions (36%), then reefs dominated by branching corals (14%). Fish assemblages differed between the reef types. Communities on soft-coral-dominated and rock/soft-coral-dominated patch reefs formed a continuum of species responses correlated with degree of soft coral cover. In contrast, branching-coral-dominated reefs were occupied by a more discrete set of species. We tested the role of soft corals in contributing to this pattern by experimentally reducing soft coral cover on patch reefs from a baseline level of ~67% to ~33% and ~6%, and monitoring the experiment over 2 years. Contrary to expectations derived from the correlative data, and in contrast with previous manipulations of hard corals, soft-coral disturbance did not generate any corresponding changes in the fish assemblage. This "negative" result indicated that the quality and heterogeneity of habitat generated by soft corals on patch reefs was indistinguishable from equiva-lent-sized habitat patches formed by bare rock alone. Nevertheless, because soft corals are living organisms they have the potential to generate indirect effects by interacting with other organisms such as hard corals. In the long-term, we hypothesize that biotic interactions between habitat forming organisms might affect composition of fish assemblages on patch reefs.

Keywords Soft corals · Reef fish · Disturbance · Habitat association

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Introduction

Distinct ecological communities are usually associated with particular habitats, which are in turn characterized by combinations of physical and biological features (Bell et al. 1991). Biotic habitat features are often subject to disturbances that generate spatial and temporal heterogeneity in the landscape (Paine and Levin 1981; Duggins 1983; Clark 1991). Spatio-temporal habitat disturbance is thus likely to drive changes in the abundance and variability of organisms within the assemblage, as they track the alteration and recovery of disturbed habitat components (Collins and Barrett 1997).

Habitat disturbance may be particularly important on coral reefs, where the biological structure of the reef constitutes the main source of habitat heterogeneity. This biological structure is dynamic in space and time, with disturbance altering habitat structure through a variety of biotic and abiotic mechanisms (Bouchon-Navaro et al. 1985; Wellington and Victor 1985; Dollar and Tribble 1993; Hughes 1994). Despite the association between coral reef fishes and the coral reef habitat, the literature provides conflicting views of how closely reef fishes are associated with habitat variables (see review in Jones and Syms 1998). Fish populations are generally highly variable (Sale 1980; Doherty and Williams 1988) and consequently the measurable association between population numbers and hypothesized habitat "preferences" may be decoupled. The apparent stochasticity of fish

populations has led to an adoption of models in which habitat does not play a prominent role in the regulation of their numbers. In these models the availability of recruits is the major determinant of community structure (Victor 1983; Doherty and Fowler 1994). Nevertheless, it has been shown that habitat mediates many processes that influence reef fish numbers (Hixon and Beets 1989, 1993), and that habitat disturbance can generate predictable shifts in coral reef fish community structure (Syms and Jones 2000).

Previous studies have quantified the relationships of hard corals with coral reef fish (see review by Jones and Syms 1998). In addition, experimental removals of hard coral cover on patch reefs have also generated strong changes in fish community structure (Syms and Jones 2000; but see Syms 1998). However, massive soft (Alcyonarian) corals also occupy a considerable amount of reef area, particularly in sheltered reef habitats (Dinesen 1983; Huston 1985; Reichelt et al. 1986), and no tests on their effects on reef fish assemblages have been conducted.

The role that soft corals play in contributing to the habitat structure of coral reefs is complex. Massive soft corals contain internal calcareous skeletal elements, and thus increase reef area both during their life and following death of the colony. The amount of reef occupied by soft corals at a locality is temporally dynamic due to differences in growth rate, susceptibility to disturbances such as storms (Van Woesik et al. 1995), and interactions with other occupants of space such as hard corals. Biotic interactions between soft and hard corals are generally aggressive, and may occur by colony overgrowth (Aliño et al. 1992; Griffith 1997) and allelopathic inhibition of settlement (Maida et al. 1995a, 1995b; Atrigenio and Aliño 1996; Griffith 1997). Mortality and growth rates of soft corals are also taxonomically variable, with both ephemeral and pioneering growth modes (e.g. some xeniids: Dinesen 1985; Benayahu and Loya 1984; and neptheid taxa: Tursch and Tursch 1982; Fabricius et al. 1995), and long-lived, slow-growing forms (e.g. alcyoniids: Fabricius 1995) forming the soft coral group.

Little is known about the association of fishes with soft corals. Some representatives of the butterflyfishes (Family: Chaetodontidae) may feed on soft coral polyps (Anderson et al. 1981; Griffith 1994), and some gobies of the genus *Bryaninops* appear to have an obligate/facultative association with massive soft corals (Randall et al. 1990). In contrast, negative associations may also occur as soft corals produce large amounts of secondary metabolites, which may have deterrent effects on predators, including fish species (Van Alstyne et al. 1994; Kelman et al. 1999). Although massive soft corals increase the total reef area, they may actually reduce the amount of shelter available to fishes by overgrowing reef crevices and thereby reducing structural complexity of the reef. Therefore, soft corals have the potential for both direct interactions with fish communities by chemical deterrence and shelter reduction, and indirect interactions by excluding hard corals or other "preferred" biotic habitat structures.

In this study, we adopted two approaches to examine the potential association between fish assemblages and soft coral communities. First, we examined how soft coral contributed to the correlative relationship between fish community structure and benthic cover of patch reefs. This enabled us to establish an estimate of the natural variability inherent in patch reef fish assemblages, and thus provide a context within which our experimental results could be interpreted. Second, we experimentally removed soft corals from soft-coral-dominated patch reefs to test their importance in structuring the fish assemblages. If soft coral cover determined community composition, then it might be predicted that disturbance of soft corals will result in a directional change in fish community composition that should mirror the correlative patterns.

Materials and methods

Natural variation in reef fish and soft coral relationships

This study was carried out at Lizard Island (14°40'S, 145°28'E) on the northern Great Barrier Reef, Australia. Sixty-four reefs of similar size and shape (2–3 m long, 0.75–1 m wide, and generally less than 1 m high) were randomly selected within a 1200-m stretch of the south-west coast of Lizard Island, and each was sampled once between the months of November 1993 and November 1994. All fish species were visually censused, and we recorded a 30-cm-wide videotape transect running over the top and around the side of the reef. Benthic cover was estimated from five random point intersects at each of 20 regularly spaced frames, to give a total of 100 point intersects per reef.

In order to differentiate naturally occurring reef types, a disjoint clustering strategy was applied to the benthic cover of the reference set of reefs using the FASTCLUS procedure in SAS (SAS Institute 1990). The clustering procedure was run for a series of cluster sizes (3–8), and the pseudo-F statistic used as the test statistic to determine the "best" number of clusters in the data set. The robustness of this solution was tested by comparison with random initial cluster seeds within FASTCLUS, and Ward's minimum variance method (PROC CLUSTER, SAS Institute 1990).

The resultant clusters defined reef types, which were used as classification variables for canonical discriminant analysis (CDA) of the fish assemblages. This enabled different reef types to be displayed in an ordination based on their fish assemblages. Plots of the structure coefficients (i.e. the correlations between fish species and the corresponding canonical variables) enabled a display of which species were characteristic of particular types of reefs. The abundances of all fish species were $x^{0.5}$ transformed for the analysis to reduce the effect of abundant species and linearize the data. The ordination effectively provided a 2-dimensional diagram in which both fish composition and the within-cluster variability of each reef could be displayed. To identify which elements of the benthic composition might have been responsible for generating the pattern, we calculated the partial correlation of each species with the main benthic cover categories.

Experimental removal of soft corals

The experiment was carried out over 24 months (July 1993–June 1995) on the sheltered south-western side of Lizard Island, within the same area as the reference set of patch reefs. A 200×300 m field of patch reefs ranging in size from 0.25 m² to >100 m² at 5–7 m depth was chosen as the study area. Seventeen patch reefs of similar size and dominated by soft corals were selected as

experimental units. Five reefs were randomly assigned to controls, and six to each of two treatment levels. Reefs were the same size as those in the survey: 2–3 m long, 0.75–1 m wide, and generally less than 1 m high. Distances between reefs were greater than 10 m, but movement of fish between reefs could not be discounted (cf. Sale 1991). Two levels of physical disturbance were applied to the reefs. The first level of disturbance consisted of removing half of the soft corals, from an initial level of 67% to 33%. The second level consisted of the removal of all soft corals from the reef (although some trace levels of soft coral cover remained).

The fish assemblage was visually sampled at ten intervals: three in the 4 months before manipulation and seven across the 20 months after manipulation. Each sample interval was a compilation of between two and three repeated censuses conducted on different days following the procedure of Sale and Douglas (1981). Recently settled recruits were distinguished from the adult population for all species. Reefs were measured and benthic cover quantified at three time intervals: immediately before manipulation, 3 months and 12 months after manipulation. As with the reference set of reefs, benthic cover was measured from a 30-cm-wide videotape transect running over the top and around the side of each reef as described previously.

The experimental design contained two fixed factors: soft coral removal and time; and consequently the appropriate test of treatment effect was the 2-way interaction (i.e. the trajectory of the community on manipulated reefs over time). As the data formed a series of repeated measures, we also included each individual reef as a blocking factor in a split-plot design to accommodate within-reef temporal structure. This approach provides an approximate guide to the amount of temporal autocorrelation (SAS Institute 1991). The data were therefore analysed with multivariate analysis of variance (MANOVA) using the model (excluding mean and error term):

Variable$_1$-Variable$_n$=Soft Coral Removal+Reef (Soft Coral Removal)+Time+Soft Coral Removal×Time

where Soft Coral Removal was tested over the blocking factor Reef (Soft Coral Removal), all other terms tested over the error, and the Soft Coral Removal×Time interaction provided the test of experimental treatment. Two orthogonal a priori contrasts within the Soft Coral Removal×Time interaction were identified and specified in the analysis. First, the temporal trajectory of controls was contrasted with that of treatments (control vs. removal); and second, the temporal trajectory of disturbance level 1 was contrasted with that of disturbance level 2 (level 1 vs. level 2 removal). To reduce analytical problems with zero values, we retained only fish species that occurred in at least 10% of samples. Abundances were $x^{0.5}$ transformed prior to analysis to linearize and normalize the data in both univariate (ascertained by normal probability plots) and multivariate space (ascertained by chi-square quantile-quantile plots of squared Mahalanobis distance).

Species richness and evenness were also calculated and analysed using univariate ANOVA of the split-plot model. We chose to analyse these parameters separately given that the correlation between richness and evenness was low ($r=-0.19$). Species richness was quantified as the number of species present on the reef, while evenness was calculated using the E_{var} index, which is independent of species richness (Smith and Wilson 1996):

$$E_{var} = 1 - \frac{2}{\pi} \arctan \left\{ \sum_{s=1}^{s} \left(\ln(x_s) - \sum_{t=1}^{s} \ln(x_t)/S \right)^2 \Big/ S \right\}$$

Recruitment data were analysed by combining total recruit numbers recorded on each reef, transforming by $x^{0.5}$, and analysing the single factor MANOVA. As in the analysis of adults, two orthogonal a priori contrasts were specified in the analysis. First, control fish assemblages were contrasted with both disturbed reef assemblages. Second, the level 1 disturbance was contrasted with the level 2 disturbance.
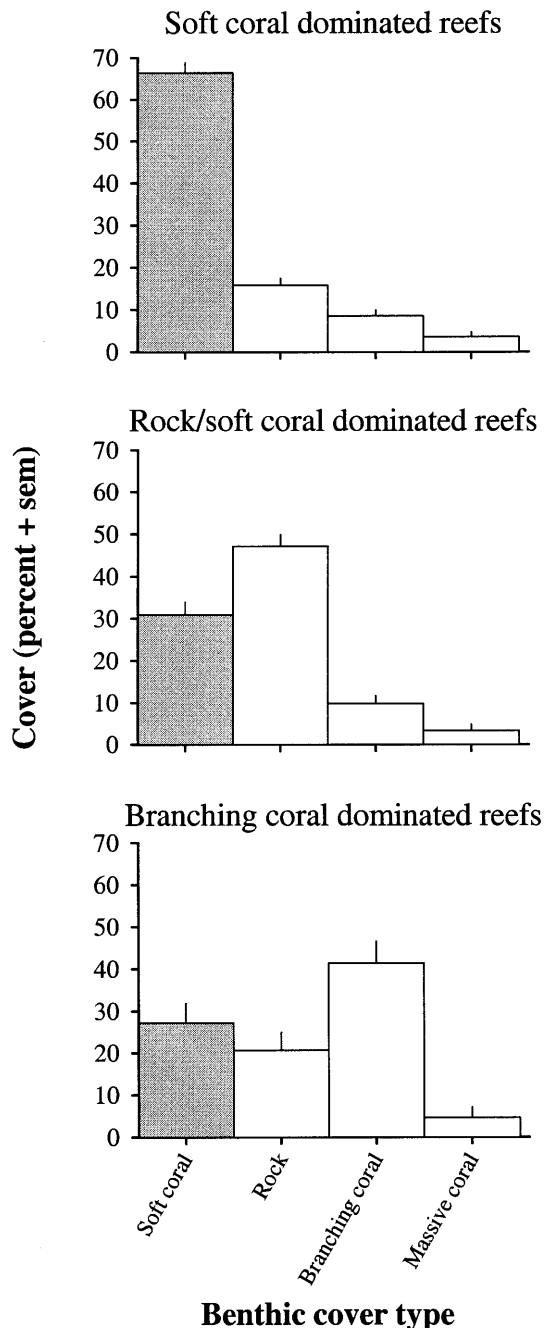

Fig. 1 Benthic composition of the three groups of naturally occurring reefs

Results

Fish community structure in relation to soft coral cover

Three types of naturally occurring reef were identified by cluster analysis of benthic cover (Fig. 1). Soft-coral-dominated reefs were the most common type ($n=32$) encountered. This group was characterized by soft coral cover dominance, smaller amounts of branching coral and rock, with residual amounts of massive hard coral covering the rest of the reef. The second most common type of reef

Table 1 Partial correlations between selected fish species ($r>|0.1|$), species richness and evenness with benthic cover of natural patch reefs

|	Soft coral	Massive corals	Branching corals
Halichoeres melanurus	0.29	–0.12	0.04
Amblyglyphidodon curacao	0.28	–0.08	–0.03
Pomacentrus amboinensis	0.22	–0.54	0.08
Cheilinus chlorourus	0.16	–0.03	0.14
Istigobius decoratus	0.11	0.16	0.08
Pomacentrus nagasakiensis	0.11	–0.11	–0.05
Neoglyphidodon melanurus	–0.12	–0.07	–0.05
Paragobiodon echinocephalus	–0.14	–0.07	0.43
Eviota sp. B	–0.17	–0.08	–0.17
Cephalopholis boenak	–0.18	–0.06	–0.04
Gobiodon citrinus	–0.19	0.13	–0.05
Eviota bifasciata	–0.20	0.00	–0.20
Premnas biaculeatus	–0.31	0.12	–0.08
Species richness	–0.08	–0.04	0.07
Evenness	–0.10	0.00	–0.13
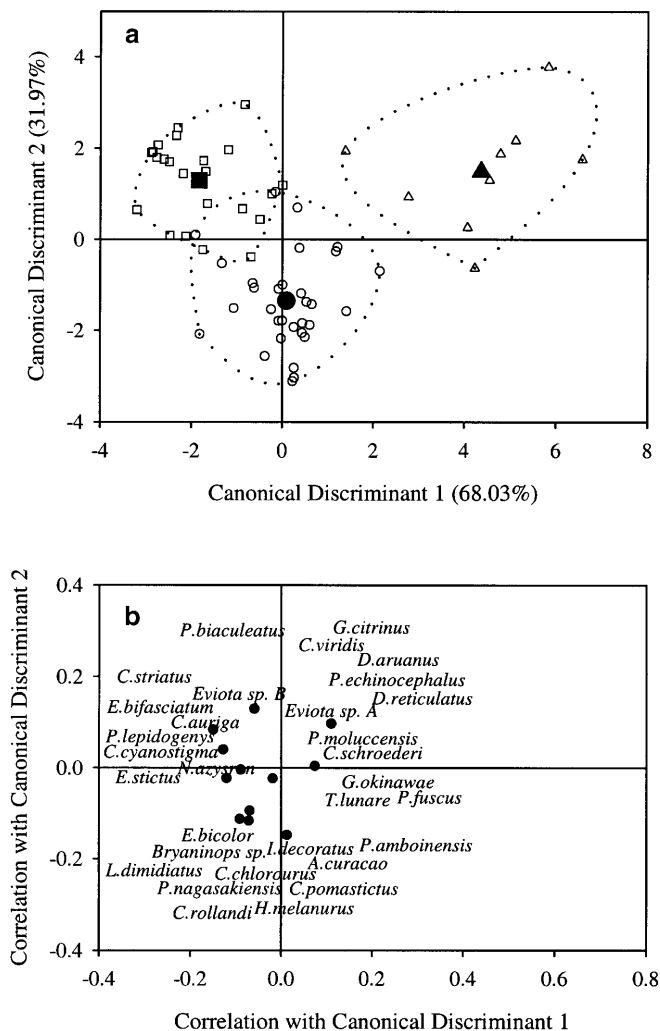
Fig. 2a, b Canonical discriminant analysis (CDA) of fish assemblages on the three groups of naturally occurring reefs. **a** The position of each reef and the centroids of the three groups (○ soft-coral-dominated reefs, □ rock/soft-coral-dominated reefs, △ branching-coral-dominated reefs). The *dashed lines* define the range of reefs within each reef type. **b** The correlation between each species and the canonical values (the structure coefficients). The *filled symbols* represent 13 species that were only weakly associated with different reef types (note one of the symbols is obscured)

($n=23$) was dominated by a combination of rock and soft coral cover, and low levels of branching coral cover. The third type of reef was far less common ($n=9$), and dominated by a combination of branching corals, soft coral and rock.

The different reef types supported characteristic, although variable fish assemblages (Fig. 2). Soft-coral-dominated and rock/soft-coral-dominated reefs represented a continuum of fish assemblages with an overlap of seven reefs. In contrast, branching-coral-dominated reefs were typically quite distinct from the other reef types. In order to determine whether the distinction between the "typical" fish assemblage on soft-coral-dominated and rock/soft-coral-dominated reefs was simply due to the contrast induced by the branching-coral-dominated reefs, we re-ran the CDA without the branching-coral-dominated reefs. The distinction between soft-coral-dominated and rock/soft-coral-dominated reef fish assemblages was maintained even in the restricted analysis, again with an overlap of seven reefs.

Soft-coral-dominated reefs were characterized by greater numbers of the pomacentrids *Chrysiptera rollandi*, *Pomacentrus nagasakiensis*, *P. amboinensis* and *Amblyglyphidodon curacao*; the labrids *Halichoeres melanurus*, *Cheilinus chlorourus* and *Labroides dimidiatus*; two sand-dwelling gobies (*Ctenogobiops pomastictus* and *Istigobius decoratus*); a soft coral/gorgonian associated goby (*Bryaninops* sp.); and a blenny (*Escenius bicolor*). As the ratio of rock to soft coral increased, fish assemblages were characterized more by an array of species including an acanthurid (*Ctenochaetus striatus*), a chaetodontid (*Chaetodon auriga*), three pomacentrids (*Pomacentrus lepidogenys*, *Neopomacentrus azysron*, and *Premnas biaculeatus*), a serranid (*Cephalopholis cyanostigma*), a blenny (*Escenius stictus*), and two gobies (*Eviota bifasciatum*, *Eviota* sp. B). Branching-coral-dominated reefs were typically quite distinct from the other groups, primarily due to the greater relative abundance of the pomacentrids *Dascyllus aruanus*, *D. reticulatus*, *Chromis viridis*, and *Pomacentrus moluccensis*; the gobies *Gobiodon citrinus*, *G. okinawae*, *Paragobiodon echinocephalus*, *Eviota* sp. A; two labrids (*Thalassoma lunare* and *Coris schroederi*), and a pseudochromid (*Pseudochromis fuscus*).

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Fig. 3a–c Benthic composition of reefs before, 3 months, and 12 months after disturbance
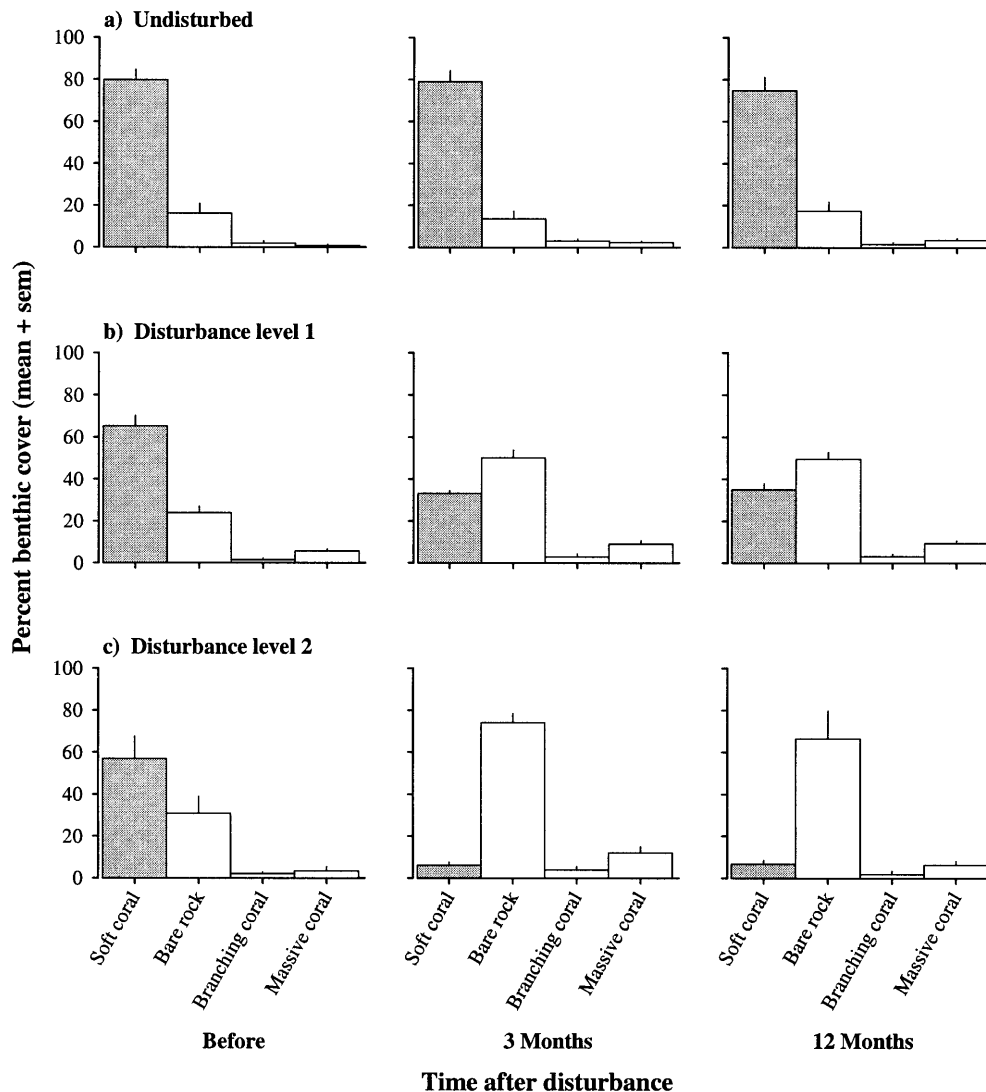
In addition to these species, 13 others were abundant in sufficient numbers for analysis but provided little discriminatory ability among different reef types (Fig. 2).

Although some fishes were associated with characteristic types of reefs, there was no a priori reason to believe that soft corals contributed to this pattern. However, partial correlations of the 44 species with the main benthic cover categories indicated that 13 species were associated with soft coral cover in particular (absolute partial correlation greater than an arbitrary level of 0.1, Table 1). This relationship was positive for six species, and negative for the remaining seven species. Consequently, reduction in amounts of soft coral would be predicted to generate different types of abundance changes in a range of species.

Experimental removal of soft corals

Disturbance effectiveness

Initial benthic cover of experimental reefs was dominated by massive soft corals from (in decreasing order of

abundance) the genera *Lobophytum*, *Sinularia*, and *Sarcophytum*. Bare and crustose algal covered rock was the next common benthic category, with massive and branching corals occupying considerably smaller proportions of reef area (Fig. 3a). Benthic cover on controls did not notably vary over time (Fig. 3a). Level 1 disturbance (50% soft coral removal) initially reduced soft coral cover from 65.33±4.92% to 33.17±1.28%; a level that was maintained for the duration of the experiment (Fig. 3b). Level 2 disturbance (100% soft coral removal) initially reduced soft coral cover from 57.00±10.64% to trace levels (6.17±1.35) and, as with the first disturbance level, these levels were maintained for the duration of the experiment (Fig. 3c). No increase in either branching or massive hard corals was observed in either treatment.

Benthic cover of experimental reefs before manipulation was typical of the most common naturally occurring category, soft-coral-dominated reefs (Figs. 2a, 3). Level 1 disturbance treatments were similar to the next most abundant natural reef type (Figs. 2b, 3). In contrast, level 2 disturbance treatments had no naturally occurring

Table 2 Analysis of variance of adult species richness and evenness using a split-plot approximation model to incorporate repeated measures

| Source	df	Type III SS	MS	F	P
Species richness					
Soft Coral Removal	2	45.3702	22.6851	0.44	0.6528 NS
Time	9	533.9950	59.3328	14.16	0.0001***
Time×Soft Coral Removal	18	101.7906	5.6550	1.20	0.1689 NS
Control vs. Removal	9	45.2910	5.0323	1.20	0.3000 NS
Level 1 vs. Level 2 Removal	9	56.5000	6.2778	1.50	0.1554 NS
Reef (Soft Coral Removal)	14	722.2533	51.900	12.31	0.0001***
Error	126	527.8800	4.1895		
Species evenness					
Soft Coral Removal	2	0.0008	0.0004	0.0175	0.9827 NS
Time	9	0.2343	0.0260	1.7972	0.0750 NS
Time×Soft Coral Removal	18	0.1703	0.0095	0.6531	0.8504 NS
Control vs. Removal	9	0.0872	0.0097	0.6700	0.7356 NS
Level 1 vs. Level 2 Removal	9	0.0831	0.0092	0.6400	0.7635 NS
Reef(Soft Coral Removal)	14	0.3469	0.0248	1.7110	0.0611 NS
Error	126	1.8249	0.0145		

*** P=0.0001, NS P>0.05
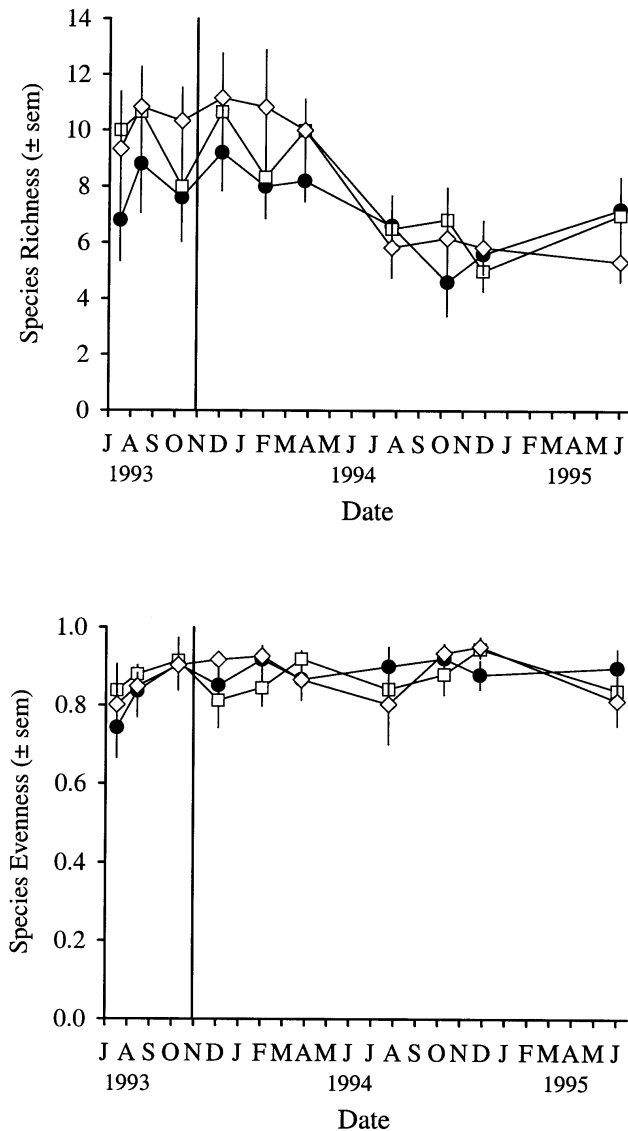
Fig. 4 Temporal changes in species richness and evenness on experimental reefs (● control, □ disturbance level 1, ◇ disturbance level 2, *vertical line* represents time of manipulation)

analog (Figs. 2c, 3). Conversely, the naturally occurring, but uncommon, set of branching-coral-dominated reefs had no experimentally induced equivalent.

Effects of experimental disturbance

Temporal patterns in assemblage composition No treatment effects were observed in any of the community measures. Species richness was not affected by manipulation (Time×Soft Coral Removal P=0.1689, Table 2), but did vary over time across reefs (Time P=0.0001, Table 2). The number of species on the reefs generally fell from 8–12 during 1993, to 6 species per reef in 1994/1995 (Fig. 4), representing a drop of one-quarter to half the resident species pool. In addition to the broad temporal changes across all reefs, a strong, temporally consistent, reef-specific effect was evident [Reef(Soft Coral Removal) P=0.001]. Evenness did not vary across the experiment (Table 2).

No compositional treatment effects were apparent but, as with species richness, composition varied over time across all reefs and individual reef-specific autocorrelation formed a large portion of explainable variation (Table 3). Because no multivariate treatment effects were detected, we plotted the abundance of the eight most abundant species through time to establish the biological significance of the result (Fig. 5). Not surprisingly, the most abundant species (with the exception of *Eviota* sp. B and *T. lunare*) on experimental reefs were those associated typically with soft-coral-dominated reefs. In addition, two species (the labrid *Coris schroederi* and the pomacentrid *Pomacentrus moluccensis*) that were typically associated with branching corals were also present in sufficient numbers for analysis. The abundance of each species was temporally variable, with the exception of the least abundant, *P. moluccensis*, which was present in low, relatively constant numbers within reefs over time, but varied between reefs within a treatment – reflecting strong reef-specific temporal autocorrelation. Although some indication of increased persistence of *P. amboinensis*

Table 3 Multivariate analysis of variance of the $x^{0.5}$-transformed data using a split-plot approximation model to incorporate repeated measures

Source	Pillai's trace	Numerator df	Denominator df	P
Soft Coral Removal	1.4815	26	6	0.7880 NS
Time	1.9133	117	1098	0.0001 ***
Soft Coral Removal×Time	1.5050	234	1638	0.8018 NS
Control vs. Removal	0.9204	117	1098	0.2994 NS
Level 1 vs. Level 2 Removal	0.6801	117	1098	0.9658 NS
Reef(Soft Coral Removal)	4.1959	182	1638	0.0001 ***

*** P=0.0001, NS P>0.05

Fig. 5 Abundances of the eight commonest species found on experimental reefs (● control, □ disturbance level 1, ◇ disturbance level 2, *vertical line* represents time of manipulation)
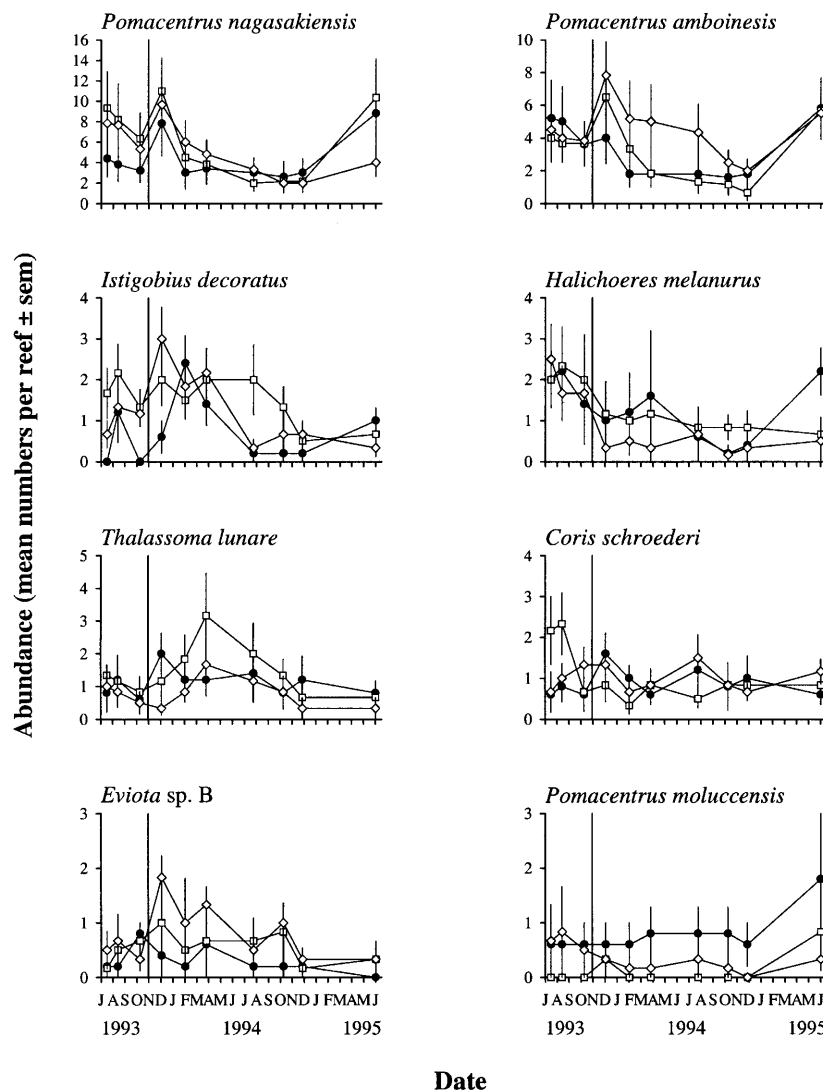
and *Eviota* sp. B on disturbed reefs was apparent, the effect was neither long-lived nor biologically important in the context of natural reef variability (Fig. 5).

Recruitment Species richness of settling fish did not differ between treatments (Table 4). Similarly, no statistically significant treatment effect on the composition of recruits was evident (Table 5), although there was a weak indication that each disturbed reef received a similar suite of recruits to each other. The weakness of this pattern could be largely attributed to variability of recruit numbers and species composition, particularly on control
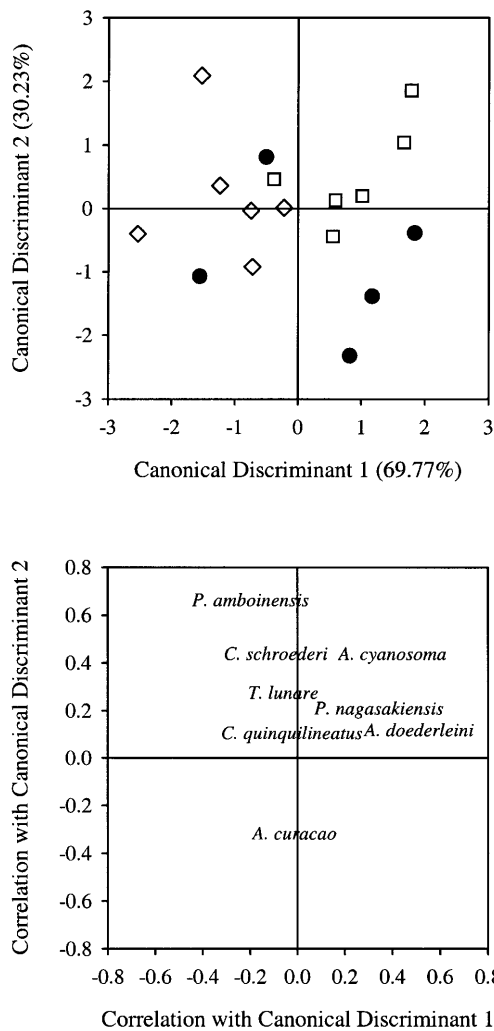
reefs (Fig. 6). Three of five control reefs and five of six reefs with level 1 disturbance received more apogonid (*Apogon doederleini* and *A. cyanosoma*), and *P. nagasakiensis* recruits. These species were effectively absent from the disturbance level 2 treatment. Control reefs were discriminated from level 1 disturbances by the presence of recruit *A. curacao*, compared with the presence of *P. amboinensis*, *C. schroederi* and *T. lunare* on level 1 disturbed reefs (Fig. 6). Recruit responses were patchy both within treatments (especially undisturbed reefs), and among species. Most of the species responsible for discriminant axes were found in high

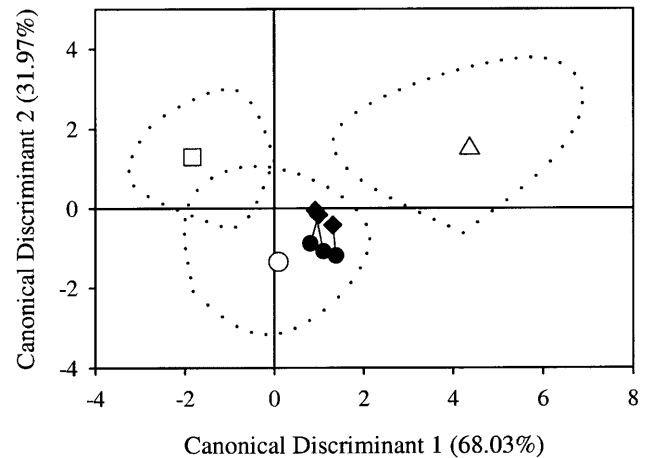**Table 4** Analysis of variance of recruit species richness across the experiment

Source	df	Type III SS	MS	F	P
Soft Coral Removal	2	4.2020	2.1010	0.33	0.7215 NS
Control vs. Removal	1	0.1186	0.1186	0.02	0.8927 NS
Level 1 vs. Level 2 Removal	1	4.0833	4.0833	0.65	0.4338 NS
Error	14	88.0333	6.2881		

NS $P>0.05$

Table 5 Multivariate analysis of variance of total recruits per reef ($x^{0.5}$-transformed)

Source	Pillai's trace	Numerator df	Denominator df	P
Soft Coral Removal	0.7794	16	16	0.8105 NS
Control vs. Removal	0.3093	8	7	0.8936 NS
Level 1 vs. Level 2 Removal	0.4780	8	7	0.6217 NS

NS $P>0.05$

Fig. 7 Evaluation of results by projection of fish composition on experimental reefs into the ordination space defined by naturally occurring reefs (○ soft-coral-dominated reefs, □ rock/soft-coral-dominated reefs, △ branching-coral-dominated reefs, ● before manipulation, ◆ after manipulation)

Fig. 6 Canonical Discriminant Analysis of total recruits/reef (● control, □ disturbance level 1, ◇ disturbance level 2)

Evaluation of the experimental manipulation No disturbance effects on fishes were found even after considerable reductions in soft coral cover. To evaluate the relevance of these results to natural patch reef assemblages, the baseline and final fish assemblages were projected into the space defined by the CDA of the natural patch reefs (Fig. 7). The starting points of all treatments were similar to each other, and well within the natural variability range of soft-coral-dominated reefs. All experimental reefs, regardless of treatment, underwent a temporal drift in species abundance and composition that, although considerable for most species (Fig. 5), was well within the range of what would be expected of fish communities on soft-coral-dominated patch reefs in that area (Fig. 7). This further supported our conclusion that the manipulation generated a result that was neither statistically nor biologically significant.

The benthic composition of the experimentally disturbed reefs (in particular the level 1 disturbance) was only superficially similar to those of the rock/soft-coral-dominated natural patch reefs. Experimental reefs differed also in their branching and massive coral cover

numbers on only a few reefs (in particular the apogonids and *A. curacao*). As a consequence, the response was not statistically significant and, given the lack of persistence of many of the species, did not generate a biologically significant effect during the course of the experiment.

Table 6 Differences between final benthic cover of experimental reefs and natural rock/soft-coral-dominated reefs. Standard errors are presented in parentheses

Treatment	Experimental cover (%)	Natural cover (%)	Difference
Soft corals			
Control	74.80 (6.34)		43.83 (6.42)
Level 1 Disturbance	35.00 (2.89)	30.97 (2.94)	4.03 (12.10)
Level 2 Disturbance	6.33 (1.78)		−24.64 (5.84)
Branching corals			
Control	1.40 (0.98)		−8.48 (3.99)
Level 1 Disturbance	3.17 (1.14)	9.88 (1.82)	−6.71 (3.66)
Level 2 Disturbance	1.83 (1.45)	−8.04 (3.76)	
Massive corals			
Control	3.40 (0.98)		0.07 (3.27)
Level 1 Disturbance	9.50 (1.18)	3.33 (1.49)	6.17 (3.01)
Level 2 Disturbance	6.33 (1.78)		3.00 (3.05)

(Table 6). All experimental reefs (including controls) had lower branching coral cover (between 7–8.5% less) than the average on the reference set of reefs sampled in the initial survey. In contrast, the massive coral cover on experimentally disturbed reefs was consistently higher (3–6%) than that on the reference set of reefs.

Discussion

Habitats are frequently defined by the faunal or floral components that contribute the most physical structure (e.g. pine forest, kelp forest, mussel beds and coral reefs). An implicit, but not unreasonable, assumption in this view is that the most obvious organisms are important in determining or regulating the abundance of other species within the system. It has been previously demonstrated that experimental disturbance of hard corals can generate strong, long-lived effects in patch-reef fish assemblages (Syms and Jones 2000). However, soft corals are also an important occupant of space on coral reefs (Dinesen 1983; Reichelt et al. 1986), and contribute to the benthic and ecological structure of reefs by generating physical structure, competing with and inhibiting settlement of other structure-generating organisms such as hard corals (Aliño et al. 1992; Maida et al. 1995a, 1995b; Atrigenio and Aliño 1996; Griffith 1997). In contrast with studies of fish association with hard corals (see review by Jones and Syms 1998), the response of fish communities to soft corals has not been examined. In this study, we found no effect of soft coral removal on fish assemblages, despite correlative evidence that soft corals might be important.

Fish assemblage structure on patch reefs strongly covaried with the amount of soft coral on the reef. We initially identified three characteristic types of reefs in the study area. Soft-coral-dominated reefs were the commonest type of reef; followed by rock/soft-coral-dominated reefs. Branching-coral-dominated reefs, which had low levels of soft coral occupancy, were far less common. Each reef type had a characteristic fish fauna, the composition of which was predictable but variable within reef types. Differences between the fish assem-blages could be attributed to particular species. Branching coral assemblages formed a relatively discrete community and were typified by recognized coral associates (Randall et al. 1990). In contrast, differences between soft-coral-dominated and rock/soft-coral-dominated assemblages represented a continuum of responses with some overlap, yet still distinguishable from each other.

Despite correlative relationships between fish species and community structure with soft coral cover, large experimental reductions in soft coral cover from ~67% to ~33% and ~6% did not generate corresponding changes in the fish assemblages. If soft corals were a strong deterministic factor regulating fish community composition, then their effect should have been measurable even above the "noise" in the system. A weak but non-significant, effect of soft coral removal was indicated in recruit availability on reefs. Control and level 1 disturbed reefs received more recruits of the apogonids *Apogon doederleini* and *A. cyanosoma*, and the pomacentrid *P. nagasakiensis*. Control reefs differed from level 1 disturbances by the presence of recruit *A. curacao*, and lower numbers of *P. amboinensis*, *C. schroederi* and *T. lunare* than on level 1 disturbed reefs. The patchiness of this response probably accounted for the lack of statistical significance and, given that there were no subsequent changes in adult numbers, biological significance.

The absence of experimentally induced changes in fish assemblage structure was surprising, and this result needs to be carefully and critically examined to determine whether this result is "negative" and hence contributes useful information, or a "non-result" resulting from an inadequate test. Correlative habitat association data strongly indicated that fish should have responded to the disturbance. Additionally, this experiment was carried out over 24 months, incorporating two fish recruitment seasons. We have found that the typical response time for patch reef assemblages to both fish removal and hard coral disturbance is generally within a few months (Syms and Jones 2000), and as a consequence the temporal scale of the experiment was sufficient for a response to occur.

The next stage in ascertaining the validity of the experimental result is to consider the likelihood of type II error. It has been suggested that non-significant tests

should be subjected to power analyses to ascertain the power of the test. There are logical flaws (Underwood 1999) and methodological caveats (Thomas 1997) in applying retrospective tests in this manner. An alternative approach would be to calculate, using the observed variance, the effect size that could have been detected for a particular level of power (Thomas 1997). However, the key test in this study was an interaction term, and we had no prior experience or intuition about how much increase in goodness of fit attributable to an interaction term would be biologically important. We believe that the result was unlikely to be due to type II error for two reasons. First, the statistical test factored out temporal (Time), pre-existing (Soft Coral Removal), and reef-specific [Reef(Soft Coral Removal)] variation from the residual thus removing as much noise as possible from the analysis. In addition, the tests were carried out with high numbers of degrees of freedom (18, 126 for the univariate test). Consequently, the key statistical test of the interaction was, a priori, likely to be powerful. Second, we ran a companion experiment (Syms and Jones 2000) in which we disturbed hard corals on similar-sized patch reefs to those used in this experiment, with similar levels of replication, at the same place and during the same time interval, analysed in the same way as in this study, and found a very strong, statistically and biologically significant Treatment×Time effect. Clearly the experimental protocol and analysis were sufficient to detect a biologically important effect, if it indeed occurred. In addition, there was no clear deviation in fish community structure on experimental reefs relative to natural reefs, and no systematic average difference in particular species on experimental and control reefs.

Two patterns, independent of experimental treatment, were evident during the course of the experiment. First, species richness and community structure varied with time. Average richness decreased following April 1994 from approximately nine to six species per reef. The numerically dominant pomacentrids, *P. nagasakiensis* and *P. amboinensis*, also decreased in abundance during this period. These temporal changes were not consistent with seasonal pattern; it appears that 1994 was simply not a good year for some species. It is possible that this large-scale temporal dynamic may have precluded a strong assemblage response to experimental disturbance. However, the same drop in richness and abundance was also recorded in the companion experiment to this one (Syms and Jones 2000), thus we believe a biologically significant effect should still have been measurable over the experiment-wide temporal dynamics. Second, there was a strong reef-specific component in both species richness and composition over the duration of the experiment. We believe this was due to a combination of unmeasured properties of reefs that result in a "characteristic" assemblage, and fish longevity resulting in the same individuals being recorded in subsequent time intervals. Given the magnitude of changes in fish abundance (and by implication, turnover) during the course of the experiment, we speculate that reef properties rather than re-measurement

of individuals accounted for the main part of this fraction of variation.

If the result was unlikely to be due to type II error, we must consider some explanations for why fishes did not respond to the disturbance of soft corals. We compared the final benthic cover of experimental reefs with the cover of the rock/soft-coral-dominated natural reefs. Experimental units differed from these reefs not only in their soft coral cover, but also in their branching and massive coral cover. All experimental reefs (including controls) had lower branching coral cover (7–8.5% less than natural levels) than that on the natural set of reefs. In contrast, the massive coral cover of disturbed reefs was consistently higher (3–6%) than on unmanipulated reefs. The magnitude, as a percentage of reef area, of these differences was low. However, when expressed as a percentage difference of the subset of space occupied by the particular benthic cover category, the differences were on the order of 22% (branching corals) to 52% (massive corals). We have argued elsewhere that percentage difference should also be considered in evaluating the importance of benthic cover in determining fish community structure (Jones and Syms 1998). It is noteworthy that hard coral cover on experimental reefs did not change following manipulation, and hence no "tracking" of the habitat by hard coral-associates would have been expected.

The demonstrable lack of habitat determinism (with respect to soft corals) does not necessarily imply that the assemblage was unorganized or chaotic. At a species presence/absence level, the species that were present at the beginning of the study persisted through two recruitment seasons. At a multivariate level, the fish assemblage on disturbed reefs, although indistinguishable from that on typical soft-coral-dominated reefs, was still distinct from branching-coral-dominated and rock/soft-coral-dominated reefs. The explainable variation in the model was subsumed by temporal and reef-specific factors implying that, despite considerable temporal variation, unmeasured reef-specific variables in combination with autocorrelation due to individual fish longevity were responsible for maintaining characteristic assemblages.

If soft corals do not exert a direct effect on fish assemblages, yet fish assemblage structure covaries with soft coral cover, what role (if any) do soft corals play in coral reef fish community structure? Reef fishes are generally more abundant in structurally heterogeneous habitats (see review by Jones and Syms 1998). Soft corals increase reef area and relief by their physical presence when alive, and they have a calcareous internal skeletal structure that may consolidate reef substratum and provide bare space following death. However, chemical deterrence (Griffith 1994; Kelman et al. 1999) and overgrowth of crevices may reduce the positive benefit to fishes. Soft corals also interact with hard corals. Competitive and aggressive interactions between soft and hard corals have been widely documented (Aliño et al. 1992; Maida et al. 1995a, 1995b; Atrigenio and Aliño

1996; Griffith 1997), and soft corals may be long-lived and thus occupy space for long periods (Fabricius 1995).

Despite the potential for competition between hard and soft corals, there was no evidence of competitive release following soft coral removal during this experiment. In addition, there appeared to be ~33% free space (i.e. rock/algae) available even on "soft-coral-dominated reefs" implying that competition for space was not strong. However, experimental studies have demonstrated that soft corals may inhibit hard coral settlement up to 65 cm away from a single colony (Maida et al. 1995a, 1995b), and colonies within 10 cm of soft corals are likely to be overgrown (Griffith 1997). We suggest that, in the presence of soft corals, the "free" space might not have been readily available for hard coral settlers. We would also predict that soft coral removal would only exert an effect if recruitment and growth of hard corals followed the disturbance. This process would probably take longer than the duration of the experiment.

A negative result can make a positive contribution to a research program. Coral reef fishes on patch reefs perceive soft corals and bare rock as equivalent, hence interchangeable substrata. The mere presence of physical structure is sufficient for certain species of fishes to become resident. Although soft corals do not have a direct effect on patch reef fish assemblages, they have the potential to assume an indirect role by occupying space and suppressing and competing with hard corals (especially branching forms). This explanation remains to be tested, but given the low rates of recruitment and slow growth of hard corals the time scale over which this process might occur would be considerably longer than the duration of this experiment. If the small absolute differences in hard coral cover of natural and manipulated patches were responsible for correlative differences in fish assemblages, this would suggest that proportional changes might be as important as absolute changes in coral cover as a measure of habitat difference. We would predict that reefs dominated by hard coral would require greater magnitude of change to generate corresponding changes in fish assemblages than would hard-coral-depauperate reefs (Jones and Syms 1998). This study provides cautions about assuming direct importance of the most conspicuously "dominant" habitat structure to organisms, and narrow interpretation of causality based only on those habitat elements that are experimentally manipulated. Habitat components may interact to generate hidden treatments, such as those postulated for terrestrial plant diversity manipulations (Huston 1997), and biotic habitat components may have temporal lags in both establishment and growth far exceeding the response and turnover time of the assemblage.

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